

- RAVEN, PETER H., O. T. SOLBRIG, D. W. KYHOS, AND R. SNOW. 1960. Chromosome numbers in Compositae. I. Astereae. Amer. Jour. Bot. 45: 124-132.
- , AND D. W. KYHOS. 1961. Chromosome numbers in Compositae. II. Helenieae. Amer. Jour. Bot. 48: 842-850.
- ROCK, H. F. L. 1957. A revision of the vernal species of *Helenium* (Compositae). Rhodora 59: 101-116, 128-158, 168-178, 203-216.
- RYDBERG, P. A. 1915-1916. Carduaceae: Tageteae. No. Amer. Fl. 34: 147-216.
- SMALL, J. 1917-1919. The origin and development of the Compositae. New Phytol. 16: 157-177, 198-221, 253-276, 1917. 17: 13-40, 69-94, 114-142, 200-230, 1918. 18: 1-35, 65-89, 129-176, 201-234, 1919.
- STEBBINS, G. L. 1950. Variation and evolution in plants. 643 p. New York: Columbia University Press.
- , J. A. JENKINS. AND M. S. WALTERS. 1953. Chromosomes and phylogeny in the Compositae, tribe Cichorieae. Univ. Calif. Publ. Bot. 26: 401-430.
- TURNER, B. L. 1954. A cytotaxonomic study of the genus *Hymenopappus* (Compositae). Rhodora 58: 163-186, 208-242, 250-308.
- , W. L. ELLISON, AND R. M. KING. 1961. Chromosome numbers in the Compositae. IV. North American species, with phyletic interpretations. Amer. Jour. Bot. 48: 216-223.
- , AND M. C. JOHNSTON. 1961. Chromosome numbers in the Compositae-III. Certain Mexican Species. Brittonia 13: 64-69.

THE PARASITIC BEHAVIOR OF  
*MELAMPYRUM LINEARE* AND A NOTE ON  
ITS SEED COLOR<sup>1</sup>

MARTIN A. PIEHL

Parasitism has been described for several members of the genus *Melampyrum*, the cow-wheats (Scrophulariaceae), beginning with *M. arvense* of Europe (Decaisne, 1847). To my knowledge, however, a parasitic existence has not been substantiated for *M. lineare*, the single North American representative of the genus. Fraysse (1906) ascribes to Heinricher (1904) the assertion that all species of the genus are parasitic; however, the latter actually said (p. 412), "Alle untersuchen Arten der Gattung *Melampyrum* sind parasitisch (*M. arvense*, *barbatum*, *nemorosum*, *silvaticum*, *pratense*)", and no reference was made to *M. lineare*. Shreve

<sup>1</sup>Contribution from the University of Michigan Biological Station.

et al. (1910) failed to find parasitic connections for *M. lineare* in Maryland but state that this plant was reportedly parasitic farther north<sup>2</sup>, and Pennell (1935) whose studies included field observations makes no mention of parasitism. The lack of information concerning this species' parasitism has received comment previously (Beauverd, 1916; Marie-Victorin, 1935).

While studying the parasitism of *Comandra*, *Pedicularis*, and other angiosperms, I have had occasion to examine *M. lineare* for comparative purposes. The majority of my observations were made during the spring and summer of 1957, 1958, and 1960 in the Mackinac Straits region, Michigan. Here *M. lineare* often occurs in dense clumps several decimeters across, suggesting seeding from one or more plants which previously grew nearby. Its characteristic habitat is open woodland, including both sandy, often dry sites under conifers and more mesic aspen stands. Rarely it occurs in bogs.

This species is an opposite-leaved annual, which in the study area is usually about 2 dm. tall at flowering, with considerable variation in height. In contrast to achlorophyllous holoparasites, e.g., *Orobanche* spp., there is no suggestion of the parasitic habit in the aerial parts of such semiparasites — the plants are green and the leaves are not proportionately smaller than those of many autotrophs. The whitish root system is shallow, consisting of a poorly defined primary root which is surpassed by some of the several lateral roots. There are comparatively few root hairs, a condition which has also been described for the European *M. pratense* (Koch, 1887). The excavated root system gives the appearance of extending only a few centimeters into the soil; however, the slender rootlets break easily, obscuring its full extent. This breakage explained my failure to find parasitic connections in the initial excavations. Minute swellings on the roots were nonetheless detected, and upon close examination some were found attached to fragments of foreign plant tissue. Later excavation was facilitated by selecting plants

---

<sup>2</sup>Additional information was not given by Shreve et al. as to when, where, and by whom this observation was made.

in loose, dry sand, and after repeated attempts involving careful brushing away of sand, a thread-like rootlet was found attached to a host root by a near-microscopic, hemispherical enlargement — the haustorium. Subsequently, it was determined that haustoria develop on essentially all plants of *M. lineare*, and that rhizomes as well as roots are parasitized. By ordinary excavation with a trowel the fragile parasite roots leading to connections were severed, leaving the haustoria attached to the host, and thus destroying direct evidence of parasitic connections. The delicateness of the attachments has undoubtedly contributed to the lack of observations on the parasitic behavior of this species.

The haustoria are developed laterally along the parent root, although at times they appear terminal because root growth beyond the haustorium has been arrested. A similar development is known for other semiparasites (Herbert, 1923; other authors). Often several haustoria develop in close succession from a single parasite root (Plate 1265, C). Unicellular, epidermal hairs develop from just above the distal end of some haustoria and may reach down to, or even extend for some distance over, the surface of the host root or rhizome (Plate 1265, D). Their development appears to be associated with the early ontogeny of the haustorium. Presumably they function as ordinary root hairs for a short time, and later may aid (very slightly) in superficial attachment of the haustorium to the host. Similar hairs occur on other species, e.g., *M. pratense* (Knorz, 1848; Koch, 1887).

Anatomically, the haustorium consists of an outer region of loosely-organized, sometimes partly-collapsed, parenchymatous cells, and a central region of compact, densely-protoplasmic cells. Through the latter region pass one or a few vessels, leading to the distal, invading portion, and eventually effecting direct continuity between the xylem of the parasite root and that of the host. I plan to discuss further anatomical details in a later report.

The haustoria are nearly circular in surface view and are ca. 0.5 (0.2-1.4) mm. in diameter, depending somewhat on the size and nature of the root or rhizome parasitized. The smaller haustoria are produced from fine rootlets with dia-

meters down to 0.1 mm. and are attached to host rootlets of about the same thickness. In general, host organs are ca. 1 mm. in diameter, although on occasion those of greater thickness are attacked. Among the largest observed were roots of large-toothed aspen (*Populus grandidentata*) 5 mm. in diameter, while those of blackberry (*Rubus cf. allegheniensis*) and the rhizomes of bracken (*Pteridium aquilinum*) were nearly as large. A maximum number of 26 haustoria per linear centimeter of host root was recorded for aspen roots of this size. Since this count was made from preserved material, even more haustoria may have been present which were unavoidably dislodged during collection. On the roughened bark of these relatively large aspen roots, haustoria tended to form in the furrows rather than on ridges, and were often insecurely attached. When sectioned, these haustoria were found to have penetrated a part of the comparatively thick bark but had not reached living tissue. Apparently the thickness and other characteristics of the bark of some hosts limit the size of roots which can be successfully attacked. When attached to larger host organs, haustoria have a slightly concave, sucker-like distal surface, while on smaller organs they are often clasping, as they partly enclose the host. Haustorial roots tend to grow parallel to large organs (Plate 1265, E), while they often contact smaller ones at an angle.

Haustorial connections to 12 species have been detected. These are taxonomically distributed over two phyla, in one of which three classes and two subclasses are involved. Eight of the hosts are dicots, but these belong to several generally diverse families. The species to which attachments have been found follow:

<i>Sphagnum capillaceum</i> (Weiss) Schrank <sup>3</sup>	
<i>Pteridium aquilinum</i> (L.) Kuhn	<i>Amelanchier cf. arborea</i>
<i>Pinus resinosa</i> Ait.	(Michx. f.) Fern.
<i>Carex pensylvanica</i> Lam.	<i>Rubus cf. allegheniensis</i> Porter
<i>Populus grandidentata</i> Michx.	<i>Gaultheria procumbens</i> L.
<i>Betula papyrifera</i> Marsh.	<i>Melampyrum lineare</i> Desr.
<i>Quercus rubra</i> L.	<i>Diervilla lonicera</i> Mill.

<sup>3</sup>Although very little material was available for identification, Prof. H. L. Blomquist believes it belongs to this species.

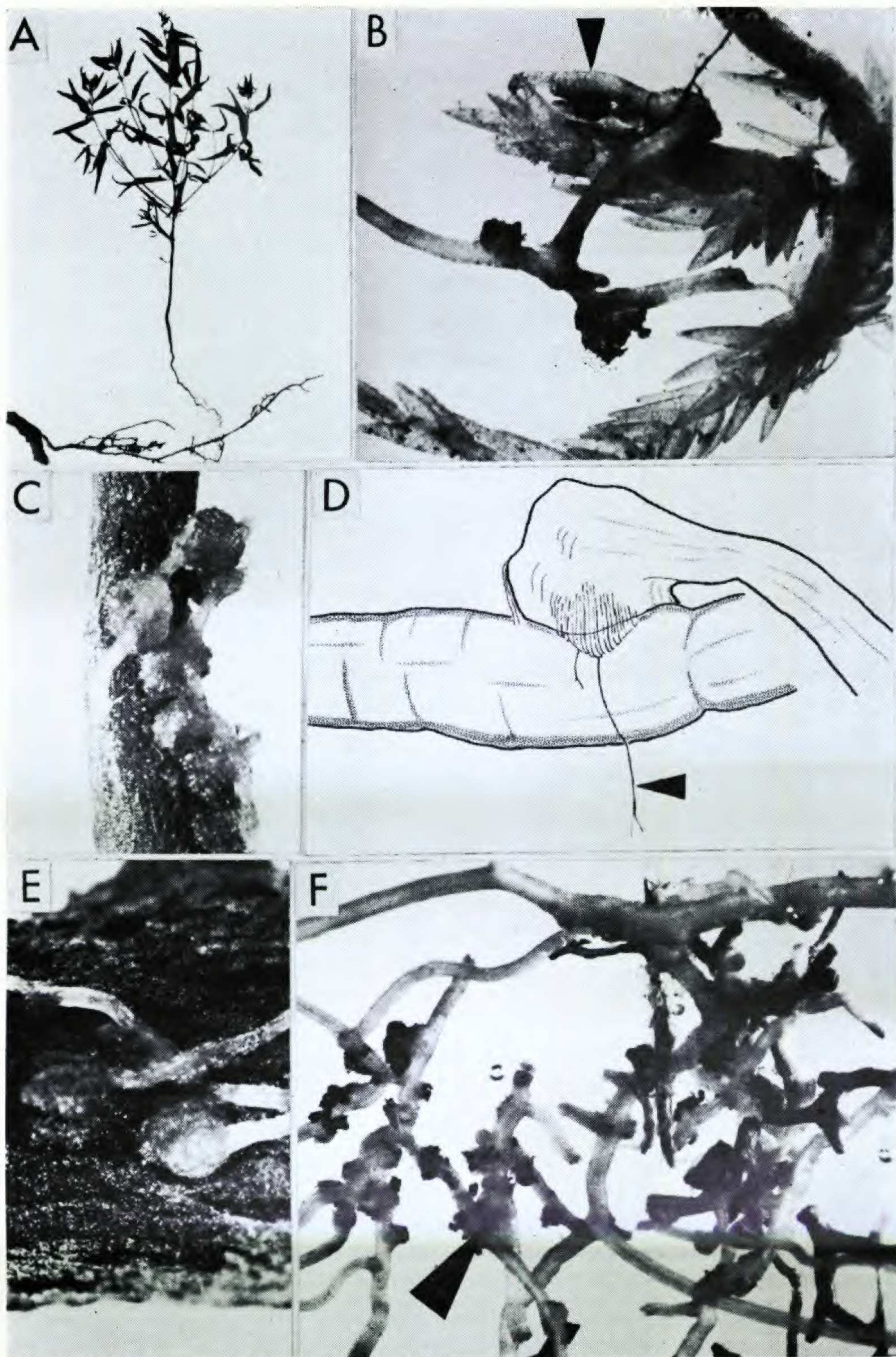


Plate 1265. Haustorial connections of *Melampyrum lineare*. A. *Melampyrum* attached to a *Pinus resinosa* root,  $\times \frac{1}{4}$ . B. Haustorial connection to *Sphagnum capillaccum* (pointer),  $\times 12$ . C. Closely successive haustoria on a *Populus grandidentata* root,  $\times 12$ . D. Single haustorium showing exceptionally strong development of hairs; a few hairs prolonged over the host root (pointer),  $\times 36$ . E. Isolated haustoria formed from *Melampyrum* roots paralleling an unusually large host root (*Populus grandidentata*),  $\times 9$ . F. Self-parasitic connection (pointer), connections to dead roots and humus (small black particles),  $\times 12$ .

Undoubtedly many more hosts can be added with further observation. The host ranges reported for several European species of *Melampyrum* are limited to gymnosperms and angiosperms (Heinricher, 1924). Heinricher also states that these cow-wheats differ from each other somewhat in their ability to grow on certain hosts.

Occasionally, I have found cases of intraspecific parasitism, where connections are formed to other individuals of *M. lineare* growing nearby. Furthermore, self-parasitism, involving other roots of a single individual, has been observed (Plate 1265, F). In general, the external features of attachment and penetration are the same here as in cases involving other species.

My single observation of *Sphagnum* as a host was made at (Inverness) Mud Lake Bog, Cheboygan County, Michigan, where haustoria were found attached to the lower achlorophyllous portion of the moss some distance below the mat surface (Plate 1265, B). Whether this should be considered a case of true parasitism is questionable, for although the upper portion of the moss was alive, the part to which haustoria were attached may have consisted wholly of dead cells. Attachments to a bryophytic host have not previously been recorded for a parasitic angiosperm.

In addition I have found numerous cases of what appears to be saprophytism, for the haustoria were attached to dead fragments of plant tissue (Plate 1265, F). These fragments can often be recognized as dead and sometimes partly decayed roots, and occasionally as other organs. In some instances haustorial connections were formed to unidentifiable humus particles. Those roots still intact, as well as the *Sphagnum* mentioned above, could have died subsequent to invasion; however, this is not possible for the already much-decayed material. Thus, living tissue is not a prerequisite for attachment. Whether substances are obtained from the dead material is unknown. This observation of attachments to dead tissues agrees with those of *M. pratense* (Knorz, 1848; Koch, 1887); however, these workers believed this species formed attachments to dead material only, and described it as saprophytic rather than parasitic. Attachments

of *M. pratense* to living plants as well have since been reported (Sperlich, 1902).

I have frequently observed some individuals of *M. lineare* in a wilted condition in nature, and as collectors soon learn, this species is one of the first to wilt, even when kept in a vasculum. I suspected that those plants which wilted easily had relatively few haustorial connections, and subsequent examination of their roots tended to verify this. This propensity to wilt, and if the drought continues, to succumb, is consistent with the observation that this species tends to be morphologically unadapted to xeric conditions; paradoxically, however, it frequents dry sandy habitats. The partial heterotrophy of this plant may well be vital to its success under such conditions.

An observation concerning seed color in *M. lineare* seems worthy of inclusion here. Although the seeds have been described as blackish<sup>4</sup> (Pennell, 1935; Fernald, 1950), I have repeatedly noted that they are beige or tan with a lighter colored tip (elaiosome according to Gislén, 1949) when released from the capsules. Ungerminated seeds found at or near the soil surface early the following spring are similarly colored, suggesting that the blackening is not a normal after-ripening change. However, seeds from herbarium specimens from various parts of the range are almost always blackish, and apparently form the basis for previous descriptions. Reference to seeds of my own specimens which were recorded as beige in the field showed that they had blackened after the specimens were dried and pressed, and germination attempts indicated such seeds were inviable. Also, some specimens blacken throughout when dried, a phenomenon which is rather common in both the *Euphrasiaeae* and *Buchnereae* sensu Pennell. Whether such a color change occurs in seeds of the European species is unknown, but if it does, an interesting etymological situation arises when one considers the generic name.

#### SUMMARY

Although previously known for European members of the

---

<sup>4</sup>Pennell describes them as brown or dark brown to blackish for ssp. *pectinatum* which is not known from northern Michigan.

genus, parasitism is substantiated for the first time for *Melampyrum lineare* Desr. from studies in Michigan. Subterranean connections of this seemingly wholly autotrophic angiosperm are established by extremely fine roots bearing minute haustoria. Invasion of the host root or rhizome ordinarily effects direct connection between the xylem of the host and that of the parasite. The hosts are taxonomically diverse — dicots, monocots, conifers, ferns, and in one instance, a bryophyte. *Melampyrum lineare* can also be self-parasitic. In addition, it forms attachments to dead plant parts and humus.

Descriptions of the seeds of *M. lineare* as blackish are believed based on dead, dried material which has blackened after collection. Mature seeds in nature have been observed to be beige or tan.

#### ACKNOWLEDGMENTS

I wish to acknowledge the helpful suggestions of Professors W. S. Benninghoff, Rogers McVaugh, W. H. Wagner, Jr., and E. G. Voss of the University of Michigan in connection with the preparation of the manuscript. — DEPARTMENT OF BOTANY, UNIVERSITY OF MICHIGAN, ANN ARBOR.

#### LITERATURE CITED

- BEAUVERD, G. 1916. Monographie du genre *Melampyrum* L. Mém. Soc. Phys. Hist. Nat. Genève 38:291-657.
- DECAISNE, J. 1847. Sur le parasitisme des Rhinanthacées. Ann. Sci. Nat. Bot. III, 8:5-9.
- FERNALD, M. 1950. Gray's Manual of Botany, 8th Ed. American Book Co., New York.
- FRAYSSE, A. 1906. Contribution à la biologie des plantes phanérogames parasites. Thesis, Univ. Paris, 178 pp. Soc. Anonyme de l'Imprimerie Générale du Midi.
- GISLÉN, T. 1949. Problems concerning the occurrence of *Melampyrum arvense* in Sweden. Oikos 1:208-234.
- HEINRICHER, E. 1904. *Melampyrum pratense* L., ein in gewissen Grenzen spezialisierter Parasit. Ber. Deutsch. Bot. Ges. 22:411-414.
- . 1924. Methoden der Aufzucht and Kultur der parasitischen Samenpflanzen. In Abderhalden, E., Ed., Handbuch der biologischen Arbeitsmethoden. Abt. 11, Teil 2:237-350.
- HERBERT, D. 1923. Phanerogamic parasites. Philip. Agric. 11:17-18.



- KNORZ, DR. 1848. Über den von Hrn. Decaisne angegebenen Parasitismus der Rhinanthaceen. Bot. Zeit. 6:239-241.
- KOCH, L. 1887. Über die direkte Ausnützung vegetabilischer Reste durch bestimmte chlorophyllhaltige Pflanzen. Ber. Deutsch. Bot. Ges. 5:350-364.
- MARIE-VICTORIN, F. 1935. Flore Laurentienne. Imprimerie de la Salle, Montréal.
- PENNELL, F. 1935. The Scrophulariaceae of eastern temperate North America. Monogr. Acad. Phila. 1:1-650.
- SHREVE, F., M. CHRYSLER, F. BLODGETT, AND F. BESLEY. 1910. The Plant Life of Maryland. Md. Weather Service, Baltimore.
- SPERLICH, A. 1902. Beiträge zur Kenntniss der Inhaltsstoffe in den Saugorganen der grünen Rhinanthaceen. Beih. Bot. Centr. 11: 437-485.

FURTHER NOTES ON THE DISTRIBUTION OF  
BIDENS CONNATA VARS.  
PINNATA AND GRACILIPES

EARL EDWARD SHERFF

Fassett (*Rhodora* 30: 31-35, Plate 160. 1928) listed the six varieties of *Bidens connata* Muhl. known to him in the State of Wisconsin: vars. *typica* (*connata*), *fallax*, *petiolata*, *ambiversa*, *anomala*, and *pinnata*. For the last of these, var. *pinnata* Wats., he listed but two collections from Wisconsin, these from Polk County (see also Aldrich & Fassett, *Science* 70: 45. 1929). Subsequently he collected, either alone or with some of his students, numerous specimens of var. *pinnata* from various other counties in northwestern Wisconsin. Through the kindness of Dr. H. Iltis of the Department of Botany of the University of Wisconsin, I have been permitted to examine those specimens critically. Moreover, in early September of 1961, I made visits to some of the localities where Fassett had collected and this permitted me to observe the living specimens in their native habitats. Suites of specimens were obtained to distribute to herbaria. As a contribution to the study of Wisconsin's flora, there follows here a condensed list of all Wisconsin specimens of var. *pinnata* studied by me. My own collections may be found represented in the Herbarium of the Chicago Natural History Museum (F); the others are in the Herbarium of the University of Wisconsin: